

DESCENT OF THE TESTIS IN THE BOVINE

by

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INTRODUCTION AND LITERATURE REVIEW

While the bovine has been employed extensively as a laboratory animal in various fields of scientific endeavor, the study of its embryogeny has been neglected. As a result no report was found in the literature on the development or descent of the testis in the bovine. Most literature dealing with the descent of the testis was directed toward mammals in general and originated from reports concerning the human (Lockwood, 1888), (Hart, 1909), (Keibel, 1912), (Arey, 1954) and the pig (Hill, 1906). Allen (1904) described the testes of mammals as arising by differentiation of the undifferentiated gonadal tissue into seminiferous tubules, rete testis, interstitial cells and stroma.

The only report in the literature concerning the embryonic development of the bovine testes was Bascom's (1923) dissertation on the development of interstitial cells in which he described testicular differentiation beginning histologically in embryos of 20 mm. crown rump measurements, becoming marked by 25 mm. The following characteristics for determining differentiation of testis from ovary were listed by Felix (1912), and Bascom (1923).

- (1) Attachment to the mesonephric body. The mesorchium is thicker than the mesovarium.

- (2) Germinal epithelium is one nucleus thick over most of the surface of the testis, two or three nuclei thick in the ovary.
- (3) Germ cells are common in the epithelium of the ovary but almost missing in that of the testis.
- (4) Regions of sex cords appeared distinctly denser than the tunica albuginea and showed some differentiation into cords in the testis, while in the ovary they were distinguished only by their irregular density.

Seminiferous cords were found to develop from sex cords (Allen, 1904) (Keibel, 1912) which formed as solid invaginations of the germinal epithelium, later became separated from it, undergoing subsequent growth by the activity of the component cells. Two types of cells were described in the sex cords: the germ-inative cells which occurred in a single layer with their bases attached to the membrane propria, and the primitive sex cells located in the more axial portions of the seminiferous cords. A thin layer of small connective tissue cells (Allen, 1904), formed a capsular investment around the membrane propria.

According to Allen (1904) and Whitehead (1904) the inter-tubular (stroma) tissue of the testis was derived from the mesothelium of the genital ridge. Whitehead (1904) described the stroma as a connective tissue syncytium consisting of cells and an exoplasmic network of fibrils. The cells were described as scarcely more than naked nuclei. The seminiferous cords were

separated from the germinal epithelium by a more compact continuation of this tissue, the tunica albuginea. Allen (1904) and Whitehead (1904) reported interstitial cells developing from the stroma cells by growth of cytoplasm in the intertubular tissue of the embryonic pig and rabbit testis. Bascom (1923) found the same in the bovine testis. The typical interstitial cell was considered to be polyhedral with a large, spherical, vesicular, and eccentric nucleus with a large nucleolus.

The rete testis was described by Allen (1904) as being developed from rete cords which arose in the anterior third of the mesonephros in the pig, and by Keibel (1912) in the human as arising from the rete blastema which was derived from a cell mass formed by the union of the inner ends of the seminiferous cords. Allen (1904) found the rete tubules connecting to ten to twelve mesonephric tubules (vasa efferentia) directly, or joining their glomeruli as the Malpighian corpuscles degenerated. Along the mediastinum of the testis the rete tubules branched into tubuli recti which united with the inner ends of the seminiferous cords (Allen, 1904; Bremer, 1911; Keibel, 1912). Bascom (1923) reported that in the bovine of 90 mm crown rump each rete tubule developed a lumen and by 115 mm was fused with the seminiferous cord. The precursors of the epididymis were described by Bremer (1911) as the anterior mesonephric tubules (vasa efferentia), while the anterior portion of the mesonephric duct formed a large part of the head, body, and tail of the

epididymis and the posterior part remained unconvoluted forming the ductus deferens.

The blood supply to the testis was described by McLeod (1958) as being furnished by the internal spermatic artery which originated from the aorta (Hill, 1906) caudal to the mesonephric arteries in the pig. The internal spermatic artery was considered to be the survivor of the mesonephric arteries in the genital region in humans (Bremer, 1911; Keibel, 1912). In the bovine it was described by Harrison (1949) as a single artery that entered the anterior pole of the testis and undulated down the posterior border to the caudal pole where it divided and subdivided forming a system of tortuous vessels over the surfaces of the testis.

The internal spermatic vein, a satellite vessel of the internal spermatic artery (McLeod, 1958) formed from venules (Harrison, 1949) which passed radially in centrifugal fashion, collected into superficial venous channels in the tunica albuginea and joined into the pampiniform plexus in the spermatic cord immediately anterior to the testis.

The nerve supply to the testis (Sisson, 1948) was derived from the renal and posterior mesenteric plexuses and formed the spermatic plexus around the vessels to which they were chiefly distributed.

Lockwood (1888), Hart (1909), Bailey and Miller (1921) described the testis of the human fetus as developing on the

medial surface of the mesonephros, covered by germinal epithelium (Hart, 1909). It was attached to the mesonephros by a fold of peritoneum, the mesorchium, between the layers of which the vessels and nerves reached the testis from the nearby parent trunks. As the mesonephros developed and projected into the body cavity it was attached to the dorsal body wall by the mesonephric mesentery. Cranial the mesentery was continued as the diaphragmatic ligament of the mesonephros, caudally it was continued to the posterior ventral body wall as the inguinal ligament of the mesonephros or inguinal fold (Nelson, 1953).

As the mesonephros atrophied, the gubernaculum formed by combination of the nephric mesentery, the mesorchium and the inguinal ligament into a single band of tissue (Bailey and Miller, 1921; McLeod, 1958; Fatten, 1958). The gubernaculum has been described as a strong band of connective tissue and smooth muscle attached cranially to the epididymis with its caudal end piercing the body wall to the corium in the inguinal region (Bailey and Miller, 1921). Hart (1909) described the caudal fibers of the gubernaculum blending in with the tissue of the processus vaginalis, with the lower tip of the processus attached to the developing scrotum by fascia. Lockwood (1888) found the gubernaculum in the human acquired attachments to the epididymis, to the testis, and to the peritoneum of the posterior abdominal wall during the third to sixth month of development. Nelson (1953) considered the gubernaculum to be a later musculo-connective tissue development of the inguinal ligament.

Bradley Patten (1946) referred to the inguinal ligament of the mesonephros as the ligamentum testis and considered it to be the cephalic portion of the gubernaculum. The caudal portion of the gubernaculum was described as a fibrous cord, the scrotal ligament, composed of the outer connective tissue layer of the recessus vaginalis and extending to the skin of the growing scrotum.

The recessus vaginalis according to Arey (1954) was formed as a pair of peritoneal evaginations in the inguinal region where the caudal end of the developing gubernaculum was attached. The recess as described by Lockwood (1888) resulted from traction applied by the gubernaculum instead of intra-abdominal forces. Keibel (1912) described the recessus vaginalis not as a true evagination but as a portion of the general body cavity narrowed by the encroachment of the neighboring parts. Each recess extended through the abdominal wall and expanded through the inguinal canal into the scrotum ahead of the testis. Lockwood (1888), Keibel (1912) and Arey (1954) reported the recessus vaginalis formed in the human during the third month of fetal development.

According to McLeod (1958) the inguinal canals consist of paired, slit-like passages through the posterior part of the abdominal floor, one on either side of the prepubic tendon. The antero-medial wall of the canal was formed by the posterior part of the internal oblique muscle. The postero-lateral wall

was formed by Poupart's ligament, a portion of the aponeurosis of the external oblique muscle. The internal inguinal ring (McLeod, 1958) was formed by the free border of the internal oblique muscle anteriorly and the upper border of Poupart's ligament posteriorly. The external inguinal ring was a slit-like opening in the aponeurosis of the external oblique muscle.

In descent (Nelson, 1953; Arey, 1954; McLeod, 1958) the testis followed the gubernaculum along the inguinal canal, behind the peritoneal tube. On reaching the scrotum the testis continued to be covered by a reflected fold of the recessus vaginalis, the tunica vaginalis propria, but was entirely outside its cavity. Hart (1909) stated the testis was never located extraperitoneally and descended into a preformed canal, the recessus vaginalis, guided by the gubernaculum which acted as a rudder instead of a tractor. Lockwood (1888), and Arey (1954) found that actual passage of the human testis through the inguinal canal began during the seventh month of fetal development. The recessus vaginalis became tunica vaginal (Lockwood, 1888; Keibel, 1912; McLeod, 1958) when it became isolated from the abdominal cavity.

Intra-abdominal descent of the testis according to Nelson (1953) may be due to enlargement of the pelvic space and increase in size of its contained structures accompanied by failure of the gubernaculum to elongate. Keibel (1912) disclaimed descent but considered its appearance to be caused by the degeneration

of organs in their cranial position while the anlagen themselves are still progressing caudally.

The external abdominal descent has been described as being the result of three primary factors.

- (1) Mechanical: The resultant shortening of the gubernaculum serves to draw the testis into the scrotum (Lockwood, 1888; Engle, 1929; Nelson, 1953).
- (2) Anatomical: The formation of the recessus vaginalis and the inguinal canal formed a funnel into which the testis could descend (Lockwood, 1888; Hart, 1909; Engle, 1929).
- (3) Physiological: Severe abdominal pressure and the action of gonadotrophic hormones may also affect testis descent (Hart, 1909; Moore, 1926; Engle, 1929; Nelson, 1953).

In an attempt to correlate and clarify the previous efforts at describing the descent of the testis, a detailed study of testis development and descent in the bovine was undertaken.

MATERIALS AND METHODS

Material for this project was secured from two sources. Eleven dated fetuses were removed from animals of the dairy herd at Kansas State University slaughtered at private abattoirs in Abilene and Salina, Kansas. Fourteen nondated fetuses were recovered from the Armour Meat Packing Company in Kansas City, Missouri.

The fetuses were removed from their fetal membranes and perfused with 10 per cent neutral formalin or a 2 per cent acetic acid 10 per cent formalin mixture as soon as possible. Perfusion was through the umbilical vessels by syringe or gravitation, depending on the size of the fetus.

Each fetus was weighed and specific measurements taken. Representative specimens were injected with red and blue latex through the umbilical artery and vein respectively, to intensify the vascular system for photography and dissection.

Each fetus was photographed before dissection, then at desired stages during dissection after relationships had been established.

The reproductive tract was removed for detailed study. Weights and measurements were taken of the epididymis, testis and gubernaculum. Slices 3 to 5 mm thick were taken from the testis, gubernaculum and spermatic cord for histological study.

The tissues were dehydrated in alcohol, embedded in paraffin and sectioned at 8 to 15 microns. The lumbar and pelvic regions of fetuses 55 and 63 days gestation were serially sectioned transversally and longitudinally. Sections were stained with a modified iron hemoxyalin and periodic acid-Schiff technic.

Fetuses recovered in the abattoirs were dated by comparison with a growth rate chart compiled from data from another phase of the study, based on body weight and length of head, hind foot, crown rump and contour.

OBSERVATIONS

55 Days

Fetus 342, removed at 55 days gestation, had metanephroi well developed* (Plate I, fig. 1), mesonephroi distinctly degenerating, testes ventral to the metanephroi, the gubernaculum present and the recessus vaginalis established. Each metanephros was 7 mm long, 3.3 mm wide and 3.2 mm thick. The metanephroi were bilaterally symmetrical, lobulated and in definitive position ventro-lateral to the second, third, and fourth lumbar vertebrae. Renal arteries and veins were established in final form and metanephric ducts (ureters) extended from the ventro-medial surface of each metanephros to the urinary bladder.

Each mesonephros occupied a space ventro-lateral to the metanephros, lateral to the second to fifth lumbar vertebrae. They were conical structures 7 mm long and 2.5 mm wide at the base, with the apical end anteriorly. The mesonephric duct was closely attached to the ventro-lateral surface of the mesonephros (Plate I, fig. 1), extending posteriorly along the dorso-lateral wall of the abdominal cavity to the urogenital sinus, and suspended by a barely visible fold of peritoneum. The anterior half of the mesonephric duct lay ventro-lateral to the ureter, crossed over to the medial side, then passed dorsally to the ureter immediately lateral to the junction of ureter and the urinary bladder.

* All plates are in the Appendix.

Table 1. Fetuses used, critical measurements and type of information obtained from each.

Number	Source	Age in Days	Weight gms.	Head Length mm.	Hind Foot mm.	Contour mm.	Crown rump mm.	Anatomical	Histological	Serial Injection Section
342	APC ¹	55	14	22	13	111	61	X	X	X
277	KSU ²	58	15.5	24	15	120	68	X	X	X
349	APC	62	24.5	27	16	145	81	X	X	X
353	APC	66	35	34	21.5	154	92	X	X	X
345	APC	72	63	33	25	163	110	X	X	X
354	APC	75	81	39	29	196	122	X	X	X
350	APC	88	226	52	39	255	165	X	X	X
126	APC	92	230	58	50	265	175	X	X	X
308	KSU	98	320	66	57	315	203	X	X	X
343	APC	101	429	64	59	305	210	X	X	X
348	APC	106	580	77	62	335	225	X	X	X
346	APC	110	670	72	65	400	235	X	X	X
347	APC	110	610	73	70	400	255	X	X	X
158	KSU	119	1070	92	87	482	298	X	X	X
295	KSU	119	1050	87	80	445	275	X	X	X
294	KSU	121	900	85	84	415	270	X	X	X
280	KSU	140	2420	99	114	567	365	X	X	X
316	KSU	151	3350	130	142	675	450	X	X	X
283	KSU	164	5052	138	164	734	540	X	X	X
136	KSU	182	9534	180	212	888	573	X	X	X
106	KSU	192	10010	200	250	1010	680	X	X	X
344	APC	205	11900	195	290	940	730	X	X	X
341	APC	210	17100	185	305	1100	730	X	X	X
329	APC	231	29510	210	360	1445	814	X	X	X
334	KSU	262	40406	265	381	1650	900	X	X	X

1. From the Armour Packing Co., Kansas City, ages determined from established growth charts.

2. From the Kansas State Dairy Herd. Known Ages.

The testes were located ventral to the anterior half of the metanephroi (Plate I, fig. 1), attached to the ventro-medial surface of the mesonephroi by the mesorchium (Plate II, fig. 1) and oriented at an oblique angle with the embryonic axis, with the posterior end directed medially. The testis was an oval body 2.5 mm long, 1.5 mm thick, weighed 4.6 mg and was composed of three distinct parts: tunica albuginea, seminiferous cords and rete testis.

The tunica albuginea was a well formed layer of connective tissue, nine to 12 cells thick, encapsulating the testis. The nuclei were oval to flattened and contained basophilic chromatin granules giving them a stippled appearance similar to mature fibroblasts. The cytoplasm contained collagenous fibers oriented parallel to the circumference of the testis. The tunica albuginea was permeated by many blood vessels which gave off branches into the stroma. It was covered by a single layer of roughly cuboidal germinal epithelial cells with large spherical basophilic nuclei containing one or two large nucleoli (Plate VI, fig. 3).

The seminiferous cords made up the cortical mass which surrounded the rete testis except anteriorly, and the tunica albuginea surrounding both. Each cord was approximately 0.05 mm in diameter and extended from the tunica albuginea to the rete testis. Any transverse section of a cord showed a surrounding layer of cells with flattened nuclei joined by thin cytoplasmic processes, enclosing a circle of five or six cells with spherical

to oblong nuclei similar to those of the germinal epithelium. One to three extremely large cells in the pachytene stage of meiosis were located randomly in the cord.

The stroma was a dense mass between the cords permeated by many blood vessels and consisting of different cell types: cells similar to those of the tunica albuginea, mesenchymal cells, and large polyhedral cells in dense clusters similar to the interstitial cells described by Bascom (1923). The latter cells had spherical vesicular nuclei with staining properties that ranged from light to dark and a granular acidophilic cytoplasm.

The rete testis appeared as a mass of irregularly arranged cells that extended postero-medially from the mesonephros, through the mesorchium, and into the lateral surface of the testis near its anterior end (Plate II, fig. 1). Cells at the anterior end of the rete mass were more regularly arranged with elongated flattened cells in longitudinal rows. In some instances nuclei were spirally arranged, hinting cord development.

The internal spermatic artery was the postero-most mesonephric artery, arising from the ventro-lateral surface of the dorsal aorta ventral to the third lumbar vertebra, continuing postero-laterally and entering the capsule of the mesonephros lateral to the anterior part of the fifth lumbar vertebra. The artery continued anteriorly in the capsule of the mesonephros to the level of the rete testis where it curved medially through the mesorchium into the tunica albuginea to the caudal pole of

the testis where it subdivided. The internal spermatic vein was formed by capillaries and venules within the stroma collecting into larger venous channels completely encircling the testis within the tunica albuginea.

The mesonephric duct was connected anteriorly with several degenerating mesonephric tubules, posterior to which it received nine, ten, or eleven tubules which curved dorsally then medio-ventrally and became continuous with the rete testis (Plate II, fig. 5). Functional mesonephric tubules joined the duct posterior to the rete. The mesonephric duct was lined by a simple cuboidal epithelium resting on a basement membrane. The lumen of the duct increased in diameter posteriorly.

The gubernaculum was 5.54 mm in length extending from the posterior tip of the testis through the wall of the abdominal cavity terminating as a thick mass beyond the tip of the recessus vaginalis (Plate VII). Within the abdominal cavity the gubernaculum was a connective tissue ligament .1 - .2 mm in diameter attached anteriorly to the caudal pole of the testis (Plate III, fig. 1), continuous for a short distance with the capsule of the mesonephric duct posterior to the testis (Plate III, fig. 2) and suspended in a posterior extension of the mesorchium which became continuous posteriorly with the connective tissue adventitia on the dorso-medial surface of the processus vaginalis (Plate III, fig. 4). Post abdominally the gubernaculum was partially surrounded by the processus vaginalis and changed gradually from a ligament to a bulbous mass ventral to the tip of the recessus vaginalis (Plate III, fig. 5).

The recessus vaginalis was a tubular extension from the postero-dorsal extremity of the peritoneal cavity directed postero-ventrally. It was approximately 1 mm long and 0.3 mm in diameter with a funnel-like opening into the abdominal cavity. The anterior portion was nearly circular in cross section with the gubernaculum within the cavity suspended from the dorso-medial surface of the processus vaginalis. Posteriorly the recessus vaginalis appeared in transverse section as a quarter-moon slit due to the intrusion of the enlarging gubernaculum (Plate III, fig. 5). The processus vaginalis was lined with peritoneum and surrounded with an adventitia of concentrically arranged connective tissue strands. The main cell component of the connective tissue consisted of immature to mature fibroblasts with oval to flattened nuclei containing many chromatin granules giving a stippled appearance in stained sections.

The processus vaginalis originated as an evagination from the posterior tip of the peritoneal cavity following the external pudic artery through the angular space between the posterior edge of the internal oblique muscle, the pubis and the prepubic tendon. This angular potential space constitutes the inguinal canal. Its postero-lateral wall was formed by the developing aponeurosis of the external oblique muscle (Poupart's ligament). Thus the processus vaginalis was peritoneum and the recessus vaginalis an extension of the peritoneal cavity.

The processus vaginalis extended from the inguinal canal through a horizontal slit (external inguinal ring) in the

aponeurosis of the external oblique muscle. The internal inguinal ring was antero-lateral to the anterior end of the pubis and was formed by the free border of the internal oblique muscle anteriorly and the upper border of Poupart's ligament posteriorly.

The scrotum at this state consisted of two minute globes on the ventral body wall between the thighs and was filled with loose mesenchymal tissue with a few scattered fibroblasts. The gubernaculum terminated dorsal to the scrotum with the mesenchyme ventral to it continuous with that filling the scrotum. There was no fibrous connection between gubernaculum and scrotum.

62 Days

Fetus 349 removed at 62 days gestation showed the testes ventro-lateral to the posterior half of the metanephroi and lateral to the third, fourth and fifth lumbar vertebrae (Plate I, fig. 2). The testes had rotated 90° on their long axes and rested immediately ventral to the degenerating mesonephroi (Plate II, fig. 4). The gubernaculum and processus vaginalis had increased in size and length with the gubernaculum now visible to the naked eye.

The metanephroi had increased in size to 8 mm long, 5.4 mm wide and 3 mm thick. The left metanephros had shifted to a position slightly posterior to the right (Plate I, fig. 2). The rapidly degenerating mesonephroi, now 4.5 mm long and 1.5 mm thick, were displaced to a position postero-lateral to the metanephroi and ventro-lateral to the fourth through sixth lumbar vertebrae.

Each testis was oval, 3 mm long, 1.6 mm thick, weighed 9 mg, and was attached dorsally by the mesorchium to the ventro-medial surface of the mesonephros. Histological preparations showed the tunica albuginea was approaching the condition of dense connective tissue with an increasing concentration of collagenous fibers, and many fibroblasts. The latter were characterized by oval to flattened nuclei with chromatin granules giving a stippled appearance. The germinal epithelium was still present but had many nuclei becoming oval to oblong and appeared to be undergoing modification.

The seminiferous cords were 0.05 to 0.06 mm in diameter and more distinct in outline than in the 55 day fetus. The cells within the periphery of the cords showed a more definite orientation perpendicular to the long axis of the cords resting on a basement membrane. Large cells in the pachytene stage of meiosis were located randomly in the cord and generally occupied the central portions of each cord. The stroma between the cords was still densely packed and consisted of mesenchymal cells, some fibroblasts, and specialized polyhedral cells which approached the characteristics of interstitial cells described by Bascom (1923). Capillaries, venules and arterioles were present in the trabeculae between the cords.

The rete testis had enlarged somewhat beyond the conditions noted for the 55 day stage and had extended more deeply into the seminiferous mass. The rete testis now extended postero-ventral through the mesorchium and due to the above described rotation

entered on the antero-dorsal surface of the testis (Plate II, fig. 3). The cellular mass of the rete testis was oriented into definite rete cords surrounded by connective tissue permeated by small blood vessels. The cords were composed of cells with condensed oblong nuclei oriented perpendicular to the long axis of the cord, with their cytoplasm filling the central core of the cord.

The recessus vaginalis had increased to 1.9 mm in length with little change except in size from the condition described for the 55 day fetus. The gubernaculum had increased to approximately 6.5 mm in length terminating dorso-lateral to the scrotum in loose mesenchymal tissue that filled the area between the peritoneal cavity and the developing abdominal wall in the area of the flank (Plate IV, fig. 5).

72 to 75 Days

The metanephroi of fetus 345 were 12 mm long, 7 mm wide and 4.5 mm thick. The right metanephros was oval in shape with the anterior tip 2 mm posterior to the last rib. The enlarging rumen had pushed the left metanephros posteriorly forcing the large anterior lobe to rotate medially and posteriorly thus compressing the hilus (Plate I, fig. 3). This pressure resulted in the left metanephros becoming triangular with the base parallel to the midline of the fetus and the apex directed towards the lateral abdominal wall.

The mesonephros was a degenerate remnant 3 x 1 mm, posterior-lateral to the metanephros. The mesonephric duct was ventro-lateral to the mesonephric remnant, following the curvature of the abdominal wall posterior-medially to the urogenital sinus. Four or five degenerating mesonephric arteries persisted retro-peritoneally across the ventral surface of each metanephros. At 72 days gestation the functional mesonephric arteries consisted of three or four lateral branches from the paired internal spermatic artery (Plate IV, fig. 4). By 75 days gestation the internal spermatic artery and vein were clearly defined, separated from the mesonephros, and larger than the degenerate mesonephric vessels. A definite plexus of veins (pampiniform plexus) was established at the anterior dorsal tip of the testis coalescing to form the internal spermatic vein.

The testes had shifted in position to the posterior-lateral edge of the metanephroi (Plate I, fig. 3), ventral to the mesonephros, suspended by a fold of peritoneum, the mesorchium. The testis was oval, 4.5 mm long, 3 mm thick and weighed 24 mg. The caput epididymis consisted of a cone shaped structure on the anterior surface of the testis comprised of 9 to 11 coiled tubules (vasa efferentia) that connected the mesonephric duct to the rete cords. The mesonephric duct extended posteriorly from this area on the dorso-lateral surface of the testis and was suspended from the lateral abdominal cavity wall by a fold of peritoneum.

Histological preparations of the testis showed the tunica albuginea to consist of an irregular connective tissue network

with many fibroblasts. It was permeated by many large blood vessels circularly arranged around the testis with perpendicular branches from the vessels extending into the stromal tissue between the seminiferous cords. The germinal epithelium was present but most nuclei were condensed and appeared oval to oblong in shape, approaching the condition of other coelomic epithelium.

The seminiferous cords had increased in length but not in diameter. They remained coiled near the periphery next to the tunica albuginea, becoming oriented radially towards the rete testis with the inner ends of the cords gradually reduced to the size of the branches from the rete cords (tubuli recti) with which they were in contact.

The rete extended deep into the testis and occupied a central area about one-third as great as the space occupied by the seminiferous cords. At the anterior end of the rete testis, cells making up the cords contained large vacuoles in the apical cytoplasm. In some areas these vacuoles appeared to coalesce forming lumens for short distances.

The gubernaculum had increased in size to 13.5 mm long and more than double in thickness over that described for 63 days. It was suspended from the dorso-lateral abdominal wall by a fold of peritoneum continuous with the mesorchium and posteriorly with the fold of peritoneum that suspended the mesonephric duct making a common fold for the mesonephric duct and gubernaculum posterior to the testis. The gubernaculum extended posterior-medially from the testis attaching to the dorsal surface of the

mesonephric duct and extending posteriorly through the internal inguinal ring to the ventral tip of the processus vaginalis.

The recessus vaginalis had expanded in length from 1.9 mm at 63 days gestation to 8 mm at 75 days gestation. It was 2 mm wide and 1.6 mm thick at its ventral extremity and 1.2 mm thick at the internal inguinal ring. The recessus vaginalis was changing shape, appearing as an elongated sac expanding around the gubernaculum. It terminated slightly above and lateral to the scrotum on either side of the penis (Plate VIII).

88 Days

Fetus 350 showed the testis posterior to the metanephroi, suspended from the postero-lateral wall of the abdominal cavity near the internal inguinal ring (Plate I, fig. 4). The left metanephros was compressed and crowded toward the midline of the fetus, the ureter extended from the medial surface posteriorly to the bladder. No position change was observed in the right metanephros. The mesonephroi appeared only on histological preparations as degenerate remnants of the Malpighian corpuscles.

The testis was oblong, 7 mm long, 3.5 mm wide, 3 mm thick and weighed 50 mg. Histological preparations showed the tunica albuginea on the dorsal surface of the testis as dense irregular connective tissue while the ventral portion maintained a looser arrangement. The germinal epithelium had been replaced by typical mesothelial cells, except for some condensed oval nuclei

on the ventral surface, forming a near typical peritoneal coat around the testes (Plate 6, fig. 3).

The seminiferous cords continued to grow in length but not in diameter. They had a definite radial orientation towards the rete testis with increased convolution, and branching near the tunica albuginea. The area between the seminiferous cords had expanded and was filled with a less dense arrangement of stromal cells.

The rete testis extended from the mesonephric tubules of the caput epididymis almost to the caudal pole of the testis and had also increased in diameter. The tubuli recti were united with the seminiferous cords along the margins of the mediastinum (Plate 6, fig. 4). The cytoplasm of the cells of the "tubuli recti" and the rete cords was heavily vacuolated giving the appearance of lumina in most of the "tubuli".

The three regions of the epididymis were established. The caput epididymis was attached to the antero-dorsal surface of the testis and consisted of the anterior portion of the mesonephric duct and the surviving mesonephric tubules (Plate I, fig. 4). The corpus epididymis was that part of the mesonephric duct along the latero-dorsal surface of the testis. The cauda epididymis was the portion of the mesonephric duct caught in the ventral surface of the gubernaculum posterior to the testis (Plate I, fig. 4). The mesonephric duct extended dorso-medially from the cauda epididymis along the medial surface of the gubernaculum as the vas deferens.

The gubernaculum had increased to 18.5 mm in length and weighed 30 mg. It was suspended within the recessus vaginalis by a peritoneal fold from the postero-medial surface of the processus vaginalis (Plate VIII). The caudal mass of the gubernaculum was now completely surrounded by the processus vaginalis and was continuous with the adventitia of the processus.

The recessus vaginalis had definitely changed its shape appearing now as an elongated sac (Plate VIII) narrow at the proximal end and widest at its distal extremity. It was 15 mm long, 2 mm wide at the internal inguinal ring, 4 mm wide at its distal extremity, extending through the inguinal canal to the level of the body wall dorsal to the scrotum.

The scrotum had changed from two globes described for the 55 day stage to a single sac-like structure suspended from the ventral abdominal wall between the thighs. The scrotal septum was well established, dividing the scrotum internally into two sacs. Connective tissue fibers developing fascia, formed a loose attachment from the bottom of the processus vaginalis to the developing corium of the scrotum.

97 to 101 Days

The right metanephros had increased in size to 22 x 12 x 8 mm but showed no change in position or shape. The left metanephros was 21 mm long, 12 mm wide, 10 mm thick and was pressed postero-ventrally along the curve of the postero-dorsal

abdominal wall (Plate I, fig. 5). The rotation described in the 75 and 88 day fetus had progressed until the anterior lobe extended across the midline into the right side of the abdominal cavity.

The testis (fetus 343) was suspended from the posterio-lateral wall of the abdominal cavity by the mesorchium with the posterior tip of the testis in position to enter the internal inguinal ring (Plate I, fig. 5). The cauda epididymis had passed through the internal inguinal ring into the recessus vaginalis. The testis was now ventro-lateral to the fifth and sixth lumbar and first sacral vertebrae.

Each testis weighed 50 mg and was 6 mm long, 4 mm wide, and 3.5 mm thick. Little change was observed histologically in the structures of the testis. The tunica albuginea was a dense irregular connective tissue network, encapsulating the testis, covered by a layer of typical peritoneum. The increase in the size of the testis appeared due to increase in stromal volume and size of the rete testis with no apparent changes in the seminiferous cords.

The cytoplasm of the cells lining the tubuli recti and the rete cords was reduced to a lattice work due to increased vacuolation. In many places these cytoplasmic processes were separated forming lumens in the developing tubules which because of the method of formation now appeared to be lined by a ragged cuboidal epithelium resting on a basement membrane. The developing tubules of the rete were surrounded by a dense

irregular connective tissue framework permeated by many blood vessels, continuous with the tunica albuginea and stroma.

The gubernaculum and the recessus vaginalis had increased to 24 mm in length with the tip of the processus vaginalis extending into the scrotum. The recessus vaginalis was 2.5 mm wide at the internal inguinal ring and 4 mm wide at the scrotal end. The gubernaculum was a white homogenous mass of collagenous connective tissue fibers which stained red with Van Gieson's stain. It was approximately 1.5 mm wide at the inguinal ring, 3 mm at its distal extremity and weighed 18 mg.

106 to 110 Days

A ventral dissection of fetus 346, 110 days gestation and fetus 348, 106 days gestation, showed no change in the position of the metanephroi, only an increase in size.

The testes had passed through the internal inguinal ring into the recessus vaginalis (Plate IX), with only the tip of the left pampiniform plexus visible in the abdominal cavity (Plate I, fig. 6). The right testis had passed through the external inguinal ring while the left testis was still in the inguinal canal. The testis, within the recessus vaginalis, was oriented perpendicular to the long axis of the fetus and suspended from the postero-medial surface of the processus vaginalis by the mesorchium. It was 7.5 mm long, 4 mm wide, 3 mm thick and weighed 65 mg.

Histological preparations showed any transverse section of a seminiferous cord with 12 to 15 cells oriented around the periphery with one to four large cells in the pachytene and diplotene stages of meiosis located randomly within the section. The developing rete tubules were approximately the same diameter as the seminiferous cords with little increase in lumen formation. The rete still occupied a large central area of the testis and extended almost to the caudal pole of the testis.

The caput epididymis formed a large oblong flattened lobe on the antero-dorsal surface of the testis due to the coiling and increasing length of its tubules (Plate VI, fig. 1). The tubules were lined by a simple columnar epithelium resting on a basement membrane surrounded by a connective tissue sheath. Slight convolutions were observed in the corpus and cauda epididymis which were lined by a simple cuboidal epithelium. The cauda epididymis was still contained within the gubernaculum ventral to the caudal pole of the testis (Plate IV, fig. 3).

The gubernaculum had increased in volume but decreased in length. It was 15 mm long, 4.5 mm wide and weighed 120 mg. Its fibers were continuous dorsally with the tunica albuginea on the ventral surface of the testis, the mesorchium and the cauda epididymis (Plate V, fig. 1). Ventrally they blended into the tip of the processus vaginalis (Plate IV, fig. 3).

The recessus vaginalis almost filled the scrotal sac and was 36 mm in length, 3 mm wide at the internal inguinal ring, and 6 mm wide at its ventral extremity. It was attached to the developing lining of the scrotum by loose fascia.

119 to 121 Days

At 119 to 121 days gestation (fetuses 158, 294, 295) the recessus vaginalis, now 51 mm long, completely filled the scrotum (Plate IV, fig. 1). The caudal poles of the testes had descended into the scrotum resting on the gubernacular mass which filled the remaining ventral portion of the recessus vaginalis.

The testis at this stage was 10 mm long, 6 mm wide, 4 mm thick, and weighed 163 mg. Histological preparations showed an increase in the size and convolutions of blood vessels within the tunica albuginea and trabeculae between the seminiferous cords. The seminiferous cords had increased in length with no histological change from the 106 day stage. Tubule formation within the rete testis was incomplete in many sections. Many of the tubuli recti were branched, uniting with two or three seminiferous cords.

The gubernaculum was 15.5 mm long, 3.5 mm thick, weighed 123 mg showing no change from the preceding stage. The processus vaginalis was composed of a mesothelial lining surrounded by a thin irregular connective tissue adventitia. External cremaster muscle fibers were present in the adventitia along the posterio-medial surface of the processus vaginalis.

The mesorchium extended from the posterior surface of the testis, enclosing the corpus epididymis and vas deferens in a common fold, and continued posteriorly becoming continuous with

the adventitia of the recessus vaginalis (Plate 5, fig. 2). The vas deferens and corpus epididymis were lined by a simple cuboidal epithelium resting on a basement membrane.

151 to 262 Days

Fetus 316 had the testes within the scrotum (Plate IV, fig. 2). The testis was 14 mm long, 8 mm wide, 7 mm thick and weighed 550 mg. Histological preparations showed the seminiferous cords greatly increased in length and convolutions. Wide spaces between the seminiferous cords were filled with a loose network of connective tissue cells and blood vessels. The large polyhedral cells of the stroma (interstitial cells of Bascom, 1923) were hard to find and generally occurred in strands between the seminiferous cords near the rete testis. Cells in the pachytene and diplotene stages of meiosis were present in the seminiferous cords. Lumen formation within the rete tubules and tubuli recti was almost complete. They were surrounded by a dense connective tissue adventitia similar to the tunica albuginea with the connective tissue spaces between the tubules permeated by large blood vessels.

The testis continued to increase in size and at 262 days gestation (fetus 334) was 33 mm long, 16 mm wide, 11 mm thick and weighed 4.1 gms.

There was a marked increase in the mass of seminiferous tubules in comparison with other structures of the testis and also an increase in size of the blood vessels contained in the

tunica albuginea. The rete tubules had expanded into sinusoids surrounded by dense connective tissue continuous with the tunica albuginea. The sinusoids were lined by a ragged, irregular epithelium composed of cuboidal and columnar cells.

Fetus 316, 151 days gestation, had the epididymis attached to the postero-medial surface of the testis by a fold of peritoneum continuous with the tunica albuginea. The cauda epididymis was compressed against the ventral tip of the testis. The epididymal tubule was slightly convoluted and lined by a cuboidal to low columnar epithelium with basally located PAS granules present in the cells. Circular smooth muscle bundles formed an adventitia around the tubule.

The gubernaculum at 164 days gestation (fetus 283) was 9 mm long, 6 mm wide and weighed 246 mg. At 231 days gestation (fetus 329) the gubernaculum appeared as a flattened compressed mass regressing into the posterior wall of the processus vaginalis. In fetus 334, 262 days gestation, the gubernaculum was completely regressed to a fibrous ligament extending from the ventral tip of the testis to the posterior wall of processus vaginalis.

DISCUSSIONS AND INTERPRETATIONS

Testis

The testis at 55 days gestation was ovoid in shape 2.5 mm long, 1.5 thick and weighed 4.6 mg. Increase in mass during the next 45 days was due mainly to an increase in size of the

rete testis and the blood vessels contained within the tunica albuginea. At 101 days gestation each testis was oblong, 6 mm long, 4 mm wide, 3.5 mm thick and weighed 50 mg. By 151 days gestation the testis was 14 mm long, 8 mm wide, 7 mm thick and weighed 550 mg; by 262 days it was 33 mm long, 16 mm wide, 11 mm thick and weighed 4.1 gms with much of the enlargement due to increase in length of the seminiferous cords as described by Bascom (1923).

At 55 days gestation the seminiferous cords were a dense compact mass of short cords 0.05 mm in diameter. They became distinctly radially arranged by 88 days but by 151 days gestation they lost the obvious radial arrangement due to an increase in length. This partially confirms the report by Bascom (1923) that no trace of the radial arrangement of the seminiferous cords appeared in fetuses of 60 cm crown rump. By 262 days gestation the seminiferous cords were still 0.05 to 0.06 mm in diameter with no lumen and appeared as a highly convoluted mass making up the bulk of the testis.

Each seminiferous cord was surrounded by flattened nuclei joined by thin cytoplasmic processes forming a thin connective sheath. Cells similar to those of the germinal epithelium at 55 days gestation, were oriented within the periphery of any transverse section of a cord and large cells in the pachytene and diplotene stages of meiosis were located randomly within the cord in all stages, increasing to three or four such cells in later stages. This is similar to the report by Allen (1904)

of two cell types in the seminiferous cords of pig embryos, germinative and primitive sex cells.

The stroma changed from a dense cellular mass in the earlier stages to a loose network of cells surrounding the seminiferous cords in later stages. Large polyhedral cells with spherical vesicular nuclei, comparable to the interstitial cells described by Bascom (1923) were present in the stroma in dense clusters at 55 days gestation. In the later stages such cells became fewer, widely separated, and progressively more difficult to identify.

The rete testis appeared as a mass of irregularly arranged cells at 55 days gestation, with cells at the anterior end of the rete mass more regularly arranged with elongated flattened cells in longitudinal rows. In some instances nuclei were spiral in arrangement hinting cord development. By 62 days gestation the cellular mass was oriented into definite rete cords composed of cells with condensed oblong nuclei oriented perpendicular to the long axis of the cord, with their cytoplasm filling the core of the cord.

By 72 days gestation branches from the rete cords, the tubuli recti described by Allen (1904) and Keibel (1912), were in contact with the inner ends of the seminiferous cords, and were united to the cords by 88 days gestation (Plate VI, fig. 4), similar to the condition described by Bascom (1923).

Lumen formation was first observed for short distances in the rete cords external to the testis at 72 days gestation by

coalescing of large vacuoles in the apical cytoplasm of its cells. This formation increased slowly and became complete by about 160 days gestation, in contrast to Bascom's (1923) report that the rete testis showed a lumen by 90 mm crown rump (about 70 days gestation). In fetuses near term the rete tubules had expanded into sinusoids surrounded by dense connective tissue continuous with the tunica albuginea, thus forming the mediastinum as recognized by anatomists.

The testis at 55 days gestation, was encapsulated by a connective tissue sheath, the tunica albuginea, which generally appeared continuous with the stroma between the seminiferous cords. The tunica albuginea developed into a dense connective tissue capsule in later stages and was permeated by many large blood vessels which produced an irregular outline on the tunica albuginea.

The tunica albuginea was surrounded by the germinal epithelium at 55 days gestation consisting of a single layer of cells with large spherical nuclei containing one or two large nucleoli (Plate VI, fig. 2). The germinal epithelium became modified to a typical mesothelial layer by 88 days forming a peritoneal coat around the testis (Plate 6, fig. 3). Hart (1909) described a similar regression of the germinal epithelium but did not consider the final result to be "peritoneum".

Epididymis

The epididymis developed from mesonephric tubules and a portion of the mesonephric duct and was divided into three distinct regions: caput, corpus, and cauda.

The caput epididymis was established by 72 to 75 days gestation as a cone-shaped structure on the antero-dorsal surface of the testis (Plate I, fig. 2) consisting of 9 to 11 mesonephric tubules and the anterior end of the mesonephric duct to which the mesonephric tubules were united (Allen, 1904; Bremer, 1911). The corpus epididymis was distinct by 88 days as that part of the mesonephric duct extending in the mesorchium along the latero-dorsal surface of the testis. The cauda epididymis was also distinct by 88 days as that portion of the mesonephric duct caught in the ventral surface of the gubernaculum posterior to the testis (Plate I, fig. 4). The mesonephric duct continued dorso-medially from the cauda epididymis as the vas deferens which connected into the urogenital sinus.

By 110 days gestation the caput epididymis formed a large oblong flattened lobe on the antero-dorsal surface of the testis due to the increased coiling of its tubules (Plate VI, fig. 1). Bremer (1911) reported that in the human, convolutions of the vasa efferentia and the ductus epididymis begin to appear at about the fourth month of fetal life. Coiling of the epididymal tubule in the corpus and cauda regions occurred at a later stage. By 151 days gestation the cauda epididymis was in close

contact with the caudal tip of the testis due to increased growth and coiling of the tubule and compression of the gubernaculum. The epididymis was lined by a cuboidal epithelium surrounded by a basement membrane in early stages with the epithelium changing to low columnar, then to columnar in later stages.

The Recessus Vaginalis and Gubernaculum

At 55 days gestation the gubernaculum and the recessus vaginalis were already established. The recessus vaginalis, was directed postero-ventrally through the inguinal ring from the postero-dorsal peritoneal cavity. It appeared as a tubular canal, 1 mm long, and 0.3 mm in diameter at the inguinal ring (Plate IV, fig. 5) diminishing gradually to a quarter moon slit at its distal extremity (Plate III, fig. 5) similar to the condition described by Lockwood (1887) for the human.

The gubernaculum was a connective tissue ligament 5.6 mm long, extending from the caudal pole of the testis posteriorly through the abdominal wall terminating as a thick connective tissue mass immediately beyond the tip of the recessus vaginalis (Plate VII). It was not attached to the scrotal wall as described by Lockwood (1888), Keibel (1912), Bailey and Miller (1921), Patten (1946), but terminated in an area of extremely loose mesenchymal tissue dorso-lateral to the scrotum (Plate IV, fig. 5). The gubernaculum was suspended in a fold of peritoneum, a posterior extension of the mesorchium, within

the abdominal cavity (Plate III, fig. 1). It was not closely applied to the dorsal abdominal wall as described by Lockwood (1888) for the human or located retroperitoneally in the abdominal wall as described by Nelson (1953). Anteriorly the gubernaculum was continuous with the tunica albuginea of the testis and with the capsule of the mesonephric duct posterior to the testis, as described by Lockwood (1888) but occurring earlier in fetal development than recognized by Lockwood. Posteriorly the gubernaculum was continuous with the connective tissue adventitia of the processus vaginalis on its dorso-medial surface and protruded into the lumen, becoming progressively larger posteriorly.

By 88 days the processus vaginalis had increased to 15 mm in length but now appeared as an elongated sac being narrow (2 mm) at the proximal end and widest (4 mm) at its distal extremity. The gubernaculum was 18.5 mm long and now completely within the recessus vaginalis as described by Hart (1909). It was suspended from the postero-medial surface of the processus vaginalis by a fold of peritoneum which diminished progressively distally (Plate VIII). The gubernaculum was now suspended by a continuous fold of peritoneum from the posterior tip of the testis to near the tip of the processus vaginalis. The change in shape of the processus vaginalis and its relationship to the gubernaculum appeared to be caused by intra-abdominal pressure forcing the processus vaginalis to balloon around and completely enclose the gubernaculum. By 88 days gestation,

loose connective tissue fibers (developing fascia) were oriented between the ventral tip of the processus vaginalis toward developing connective tissue lining of the scrotum, not however, forming any sort of a tractile cord such as described by Bailey and Miller (1921), Patten (1946), McLeod (1958).

The processus vaginalis continued to increase in length so that by 101 days gestation each processus was approximately 24 mm long with the ventral tip extending into the scrotum. By 121 days gestation it was 51 mm long and completely filled the scrotum, containing the regressing gubernaculum, the testis attached to the posterior wall by the mesorchium, and the vas deferens.

The gubernaculum continued to increase in length as the testes migrated through the abdominal cavity, reaching its greatest length observed, 24 mm, by 101 days gestation. As the testis descended within the recessus vaginalis the gubernaculum, consisting of a homogenous mass of collagenous connective tissue fibers, shortened progressively to 15.5 mm at 121 days and 8 mm at 164 days gestation. The gubernaculum was becoming incorporated into the adventitia of the posterior wall of the processus vaginalis at 231 days and remaining only as a fibrous connection between the testis and the processus vaginalis by 262 days gestation.

Histologically the processus vaginalis had a mesothelial lining surrounded by concentrically arranged connective tissue

strands forming a thin adventitia. Isolated muscle fibers, derived from the internal oblique muscle, appeared in the dorso-medial region of the adventitia at 55 days gestation forming the anlage of the external cremaster muscle.

The gubernaculum was composed of loosely arranged collagenous connective tissue fibers which stained red with Van Giesen's stain. No smooth muscle fibers were found in the gubernaculum in contrast to the reports of Lockwood (1888), Keibel (1912), Bailey and Miller (1921) and Nelson (1953).

Descent of the Testis

The descent of the testis was rather distinctly divided into two phases; (1) posterior migration within the abdominal cavity (2) ventral descent within the recessus vaginalis.

At 55 days gestation the testes were located ventral to the anterior half of the metanephroi (Plate I, fig. 1). They were attached to the ventro-medial surface of the mesonephroi by the mesorchium (Plate II, fig. 2) and were oriented at an oblique angle with the embryonic axis with the posterior end medial to the anterior.

By 62 days gestation the testes had shifted to a position ventro-lateral to the posterior half of the metanephroi and lateral to the third to fifth lumbar vertebrae (Plate I, fig. 2). The testes had rotated 90° on their long axes and rested immediately ventral to the degenerating mesonephroi (Plate II, fig. 4). Continued degeneration of the mesonephros anteriorly

and intra-abdominal pressures were probably factors involved in the rotation of the testis which was now in the position to be maintained during its migration posteriorly in the abdominal cavity.

The testes were posterior to the metanephroi by 88 days gestation (Plate I, fig. 4) and by 101 days gestation the posterior tip of the testis was flush with the inguinal ring (Plate I, fig. 5), ventro-lateral to the fifth and sixth lumbar and first sacral vertebrae. Migration was within the abdominal cavity by modification of the mesorchium as described by Hart (1909) and not retroperitoneally as reported by Bailey and Miller (1921), Arey (1954) and Nelson (1954).

This change in position was due to active migration of the testis posteriorly through the abdominal cavity and not a passive shifting in relative position as reported by Lockwood (1888) and Keibel (1912) due to growth of structures in relationship to the testis while it remained stationary. Active migration was established by following the relationship of the testis to the metanephros and to the lumbar vertebrae. At 55 days the testis was ventral to the anterior half of the metanephros and lateral to the second to fourth lumbar vertebrae. By 62 days it was ventro-lateral to the posterior half of the metanephros and lateral to the third to fifth lumbar vertebrae. The testis was posterior to the metanephros by 88 days. By 101 days the testis was ventro-lateral to the fifth and sixth lumbar and the first caudal vertebrae. The right metanephros was at 55 days

in its definitive position just posterior to the last rib and anterior to the fifth lumbar vertebrae while the left metanephros shifted posteriorly as described previously. Thus shifting of relative position of testis to metanephros cannot be logically ascribed to metanephric changes.

The gubernaculum seemed to play a two-fold part in the migration of the testis: (1) it acted to anchor the testis to the posterior tip of the processus vaginalis (Plate IV, fig. 3) and (2) it served to guide the testis during migration. Only Hart (1909) suggested the latter function of the gubernaculum. Other authors Lockwood (1888), Patten (1946), and Nelson (1953) considered it to serve as a contractile structure.

The abdominal migration of the testis occurred between 55 and 101 days gestation while the fetus increased in overall length from 61 to 210 mm. In the meantime the gubernaculum increased in length from 5.6 to 24 mm but the processus vaginalis increased from one to 24 mm. As the gubernaculum was attached firmly to the wall of the processus vaginalis, any expansion of the processus resulted in direct tension on the gubernaculum, thus drawing the testis toward and into the recessus vaginalis.

As the preceding described changes took place the mesorchium also underwent modification. The testis and the gubernaculum were suspended within the abdominal cavity by a continuous thin sheet of mesorchium, not located retro-peritoneally as has been assumed by Nelson (1953), Arey (1954), and McLeod (1958). The tension exerted by the gubernaculum

directly affected the mesorchium. As the testis was drawn posteriorly the mesorchium was stretched out anteriorly and compressed posteriorly resulting in progressive modification.

The recessus vaginalis continued to increase in size (from 24 mm at 101 days to 36 mm at 106 days) forming the passage way for the ventral descent of the testis. The gubernaculum in the meantime shortened to 15 mm. These factors plus intra-abdominal pressure forced the testis through the inguinal ring into the recessus vaginalis. As the testis passed through the internal inguinal ring it passed almost simultaneously through the external inguinal ring which was slightly ventro-lateral to the internal ring. Once inside the recessus vaginalis a new force combined with that of the intra-abdominal pressure in exerting force on the descending testis. This force came from the tension on the aponeurosis of the external oblique muscle and abdominal tunic postero-ventrally, while the intra-abdominal pressure exerted force from the dorsal aspect resulting in a modified peristaltic action on the recessus vaginalis. This coupled with (1) increased length of the recessus vaginalis while (2) the gubernaculum regressed and (3) an increase in the size and weight of the testis together with (4) constant abdominal pressure exerting force, the testis came to rest within the scrotum by 151 days gestation.

The testis was directly encapsulated by the original tunica albuginea which persisted throughout the migration and descent. The tunica albuginea originated from the genital ridge and was

continuously covered by a coelomic epithelium, originally the germinal epithelium. The tunica albuginea was connected to the recessus vaginalis only by the mesorchium. There was no addition to the tunica albuginea of a reflected layer of peritoneum from the posterior wall of the processus vaginalis as reported by Nelson (1953) and McLeod (1958). Therefore, the layer around the testis called "tunica vaginalis propria" never was part of the vaginalis, but is only the peritoneal portion of the albuginea.

The processus vaginalis could now be referred to as the tunica vaginalis. It was not a part of the wall of the scrotum but a closed sac lined by a serous membrane which was continuous with that of the peritoneal cavity. It contained the testis and the spermatic cord which were attached to the posterior wall by the mesorchium. There can be no rational subdivision of this tunic into tunica vaginalis propria and tunica vaginalis communis as is commonly done by anatomists (Sisson, 1948; McLeod, 1958).

SUMMARY

In a study of testis descent in the bovine, 25 fetuses, 55 to 262 days gestation, were used. The fetuses were dissected and photographed, and sections for histological study removed as deemed necessary.

At 55 days gestation the testis was differentiated: the rete testis, gubernaculum, recessus vaginalis, internal spermatic artery and vein, inguinal canal, internal and external inguinal rings and the scrotum were established.

The testis was oval in shape, weighed 4.6 mg at 55 days becoming progressively more elongate and weighed 4.1 gm. by 262 days gestation. The tunica albuginea and the germinal epithelium were present at 55 days with the germinal epithelium were present at 55 days with the germinal epithelium modified to a typical coelomic epithelium around the testis by 88 days gestation.

The seminiferous cords were a dense mass of short cords at 55 days, becoming radially arranged by 88 days and a convoluted mass by 151 days gestation. The cords remained 0.05 to 0.06 in diameter with no lumen. Lumen formation in the rete cords was first observed at 72 days gestation at the anterior end of the rete, and gradually became complete within the testis by about 160 days.

The three regions of the epididymis were established by 88 days gestation. The caput epididymis consisted of nine to eleven mesonephric tubules and the anterior end of the mesonephric duct located on the antero-dorsal surface of the testis. The corpus epididymis consisted of the portion of the mesonephric duct caught in the ventral surface of the gubernaculum posterior to the testis.

The gubernaculum, present as a connective tissue ligament at 55 days, changed to a homogenous mass of collagenous connective tissue fibers by 121 days. The gubernaculum increased in length from 5.6 mm to 24 mm as the testis descended within the recessus vaginalis, forming a fibrous connection

between the testis and the wall of the tunica vaginalis by 262 days gestation. The recessus vaginalis formed a passageway into which the testis descended, and filled out the scrotum by 121 days gestation.

Testis descent was divided into two phases (1) posterior migration within the abdominal cavity, (2) ventral descent within the recessus vaginalis. The testis ventral to the anterior half of the metanephros at 55 days gestation, migrated posteriorly to the internal inguinal ring by 101 days gestation. The testis was suspended within the abdominal cavity by the mesorchium and did not migrate retroperitoneally. Disproportionate increases in length between the gubernaculum and the recessus vaginalis were probably the factors in this process. The gubernaculum was attached firmly to the wall of the processus vaginalis and as the processus expanded tension resulted on the gubernaculum drawing the testis towards and into the recessus vaginalis.

The testis passed through the inguinal ring into the recessus vaginalis by 106 days and by 151 days had settled into the scrotum. Five main factors appeared to be involved in the passage through the inguinal ring and in further descent; (1) intra-abdominal pressure coupled with (2) increased length of the recessus vaginalis while (3) the gubernaculum is shortened (4) pressure from the aponeurosis of the external oblique muscle and the abdominal tunic and (5) increase in size and weight of the testis itself.

The processus vaginalis could be referred to as the tunica vaginalis with the descent of the testis into the scrotum. There can be no rational subdivision of this tunica into tunic vaginalis propria and communis since the testis was encapsulated by the original tunica albuginea which was covered by a coelomic epithelium, originally the germinal epithelium.

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APPENDIX

ABBREVIATIONS USED IN THE PLATES

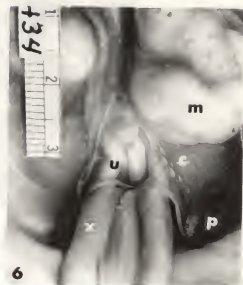
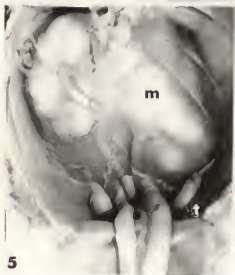
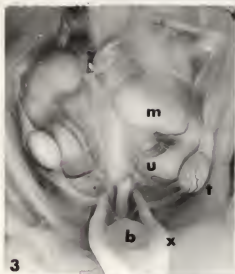
UB, b	Bladder
bv	Blood vessel
a	Dorsal aorta
E	Epididymis
Ep ₁	Epididymis, caput
Ep ₃	Epididymis, cauda
ge	Epithelium
Er	External inguinal ring
G	Glomeruli
Gub, g	Gubernaculum
Er	Internal inguinal ring
c	Internal spermatic artery
Mes, n	Mesonephros
d	Mesonephric duct
N	Mesonephric tubules
Mo, o	Mesorchium
Met, m	Metanephros
p	Pampiniform plexus
Pen	Penis
Pc	Peritoneal cavity
P	Processus vaginalis
Pu, Pub	Pubis
R, v	Recessus vaginalis
r	Rete testis
Sc, s	Scrotum
h	Seminiferous cord
T, t	Testis
tr	Tubuli recti
ta	Tunica albuginea
tv	Tunica vaginalis
x	Umbilical artery
Ve, u, e	Ureter
Ur	Urethra
VD, vd	Vas deferens
Ver	Vertebrae

EXPLANATION OF PLATE I

Ventral dissection of male fetuses showing relationships of urogenital organs during the abdominal migration of the testis.

- Fig. 1. Fetus 342, 55 days gestation showing the relationship of testis, metanephros, mesonephros, and mesonephric duct.
- Fig. 2. Fetus 349, 62 days gestation, with testis ventro-lateral to metanephros.
- Fig. 3. Fetus 354, 75 days gestation, with testis in position posterior to metanephros.
- Fig. 4. Fetus 350, 88 days gestation, with testis mid-way between metanephros and internal inguinal ring.
- Fig. 5. Fetus 343, 101 days gestation, with testis at the internal inguinal ring.
- Fig. 6. Fetus 346, 110 days gestation, with only the pampiniform plexus visible in abdominal cavity.

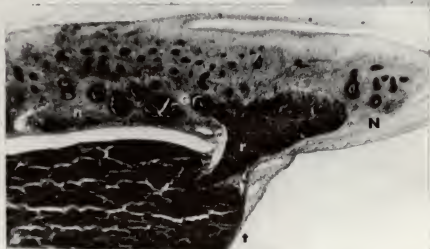
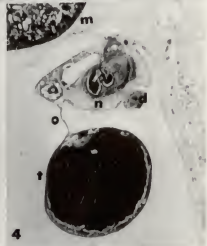
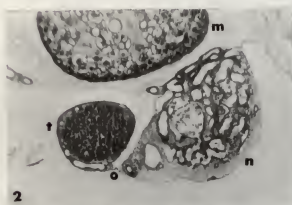
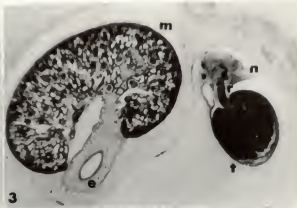
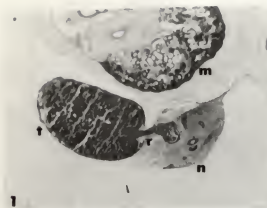
PLATE I



EXPLANATION OF PLATE II

- Fig. 1. Transverse section of fetus 342, 55 days gestation, near the anterior end of metanephros, mesonephros, rete testis, and testis.
- Fig. 2. Transverse section of fetus 342 posterior to fig. 1 showing relationships of the mesorchium to testis and mesonephros.
- Fig. 3. Transverse section of fetus 349, 62 days gestation, near the anterior end of the mesonephros showing the ventro-lateral rotation of the testis.
- Fig. 4. Transverse section of fetus 349 posterior to fig. 3 showing the relationships of the mesorchium to the mesonephros and testis.
- Fig. 5. longitudinal section of fetus 349 showing relationship of testis, rete testes, mesonephros, glomeruli, and mesonephric tubules.

PLATE II

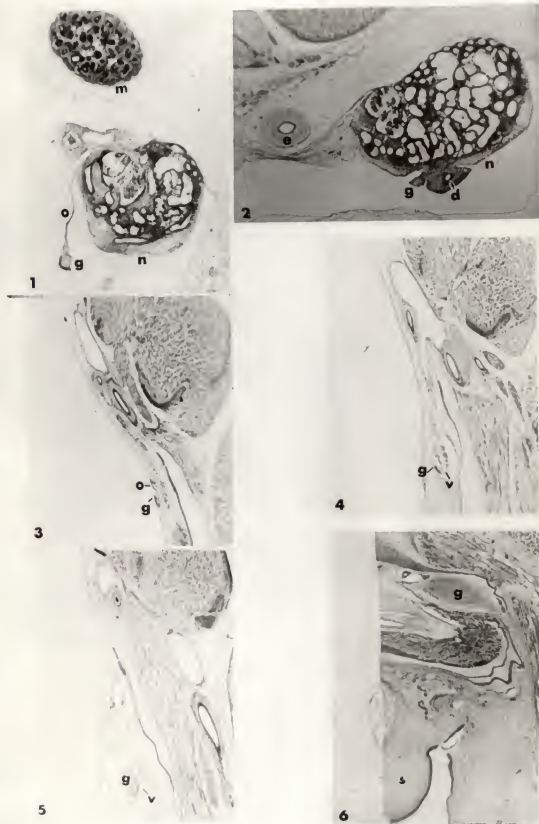


EXPLANATION OF PLATE III

Transverse section of fetus 349, 63 days gestation, showing relationships of the gubernaculum throughout its length. Magnification approximately 20X.

- Fig. 1. Gubernaculum (g) just posterior to testis suspended by the mesorchium (o).
- Fig. 2. Connection of gubernaculum to the capsule of mesonephric duct (d) posterior to fig. 1.
- Fig. 3. Position of gubernaculum at the internal inguinal ring.
- Fig. 4. Suspension of gubernaculum by the mesorchium within the recessus vaginalis (v).
- Fig. 5. Thickening of the gubernaculum near the distal tip of the recessus vaginalis.
- Fig. 6. Termination of the gubernaculum dorsal to the scrotum.

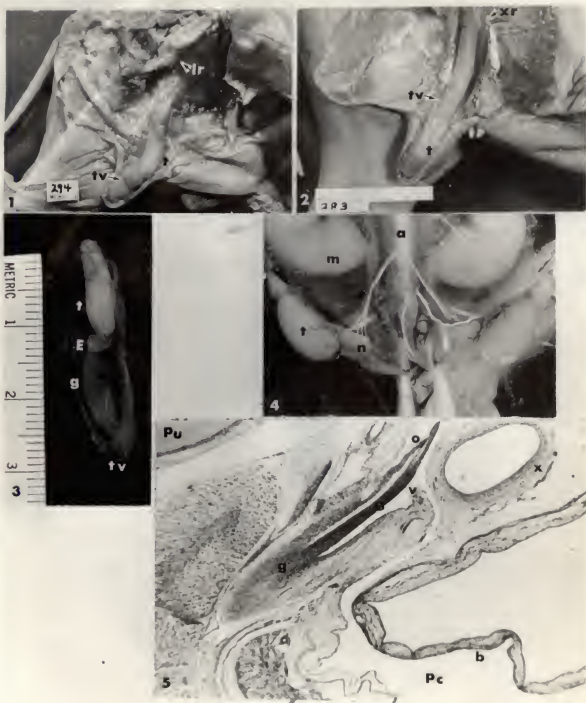
PLATE III



EXPLANATION OF PLATE IV

- Fig. 1. Lateral dissection of fetus 294, 121 days gestation, showing the testis within the tunica vaginalis passing into the scrotum.
- Fig. 2. Lateral dissection of fetus 283, 164 days gestation, showing the testis in the tunica vaginalis with the scrotum.
- Fig. 3. Lateral view of the dissection of the partially descended testis and associated structures from fetus 346, 110 days gestation, showing the attachments of the gubernaculum (g) and the position of the cauda epididymis (E).
- Fig. 4. Ventral dissection of fetus 345, 72 days gestation, showing the branching of the internal spermatic artery as it enters the mesonephric capsule (n).
- Fig. 5. Longitudinal section of fetus 349, 62 days gestation, showing relationship of gubernaculum, mesorchium (o), and recessus vaginalis (v). Magnification approximately 40X.

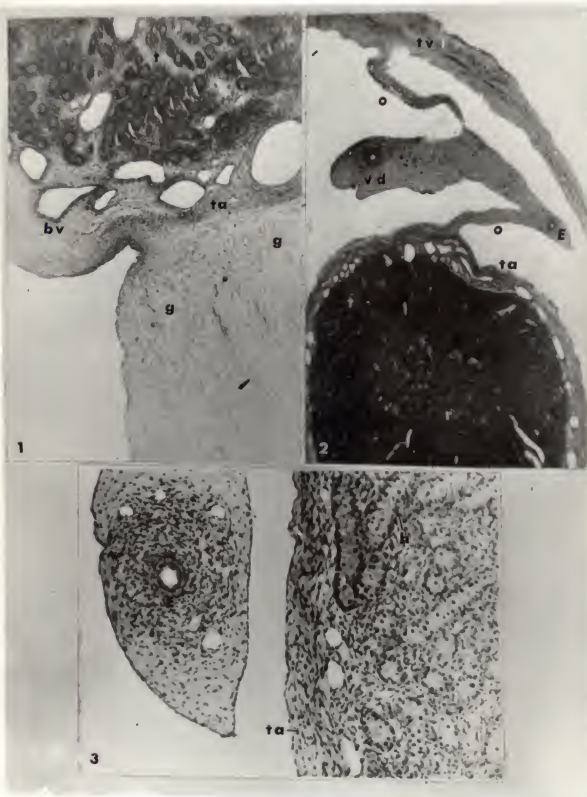
PLATE IV



EXPLANATION OF PLATE V

- Fig. 1. Longitudinal section showing the attachment of the gubernaculum to the caudal pole of the testis, from fetus 346, 110 days gestation.
- Fig. 2. Transverse section of the testis showing its relationship to mesorchium (o), vas deferens (vd), and tunica vaginalis (tv), from fetus 158, 119 days gestation.
- Fig. 3. Transverse section of the testis, showing seminiferous cords (h) and corpus epididymis (E) from fetus 350, 88 days gestation.

PLATE V



EXPLANATION OF PLATE VI

- Fig. 1. Transverse section, fetus 346, 110 days gestation, showing relationships of the rete testis (r) to the caput epididymis (E), mesonephric tubules (N), and the testis (T).
- Fig. 2. Transverse section of the epithelium of the testis, fetus 350, 88 days gestation.
- Fig. 3. Transverse section of the epithelium of the testis, fetus 342, 52 days gestation.
- Fig. 4. Longitudinal view of the seminiferous cord (h), tubule recti (tr), and "rete tubules" (r), fetus 350, 88 days gestation.
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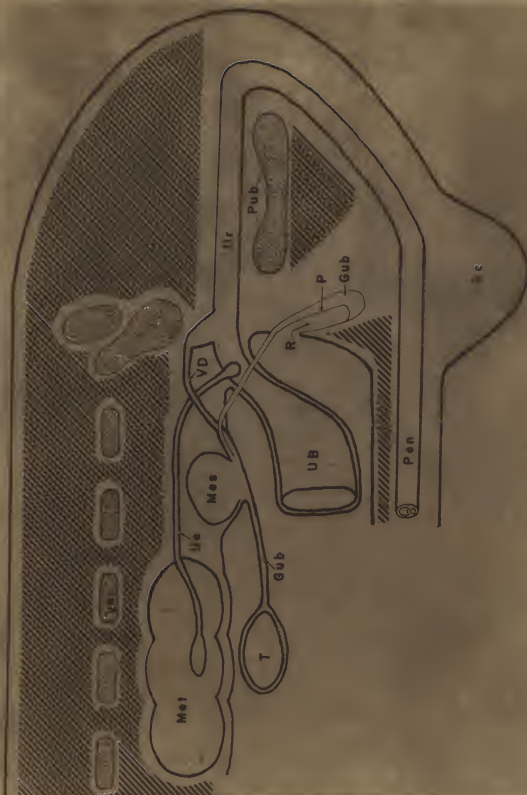
PLATE VI



EXPLANATION OF PLATE VII

Diagrammatic drawing showing a longitudinal view of the relationships of the urogenital organs of a fetus approximately 62 days gestation.

PLATE VII



EXPLANATION OF PLATE VIII

Diagrammatic drawing of the relationship of the urogenital organs of a fetus, approximately 88 days gestation.

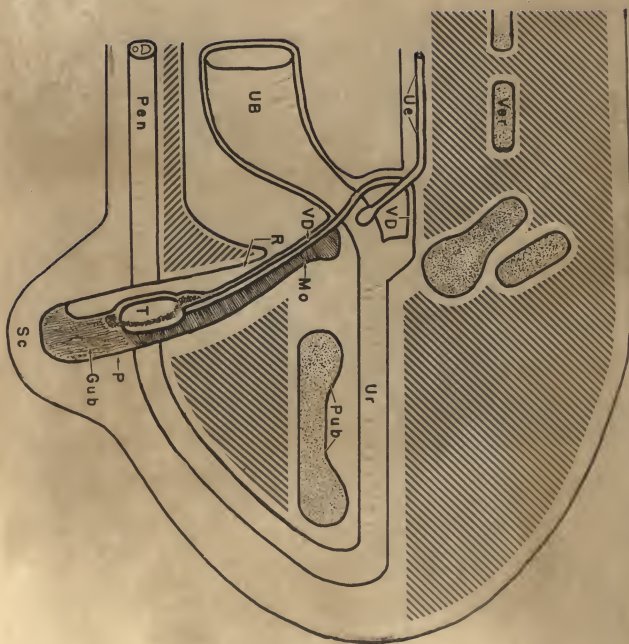
PLATE VIII



EXPLANATION OF PLATE IX

Diagrammatic drawing of the relationship of the urogenital organs of a fetus approximately 120 days gestation.

PLATE IX



DESCENT OF THE TESTIS IN THE BOVINE

by

EUGENE BILLY KREHBIEL

B.S., Bethel College, 1957

AN ABSTRACT OF A THESIS

submitted in partial fulfillment of the
requirements for the degree

MASTER OF SCIENCE

Department of Zoology

KANSAS STATE UNIVERSITY
Manhattan, Kansas

1961

A review of the literature was made and no report was found on the development or descent of the testis in the bovine.

In a study of testis descent in the bovine, 25 fetuses, 55 to 262 days gestation, were used. The fetuses were dissected and photographed, and sections for histological study removed as deemed necessary.

At 55 days gestation the testis was differentiated: the rete testis, gubernaculum, recessus vaginalis, internal spermatic artery and vein, inguinal canal, internal and external inguinal rings and the scrotum were established.

The testis was oval in shape, weighed 4.6 mg at 55 days becoming progressively more elongate and weighed 4.1 gm by 262 days gestation. The tunica albuginea and the germinal epithelium were present at 55 days with the germinal epithelium modified to a typical coelomic epithelium around the testis by 88 days gestation.

The seminiferous cords were a dense mass of short cords at 55 days, becoming radially arranged by 88 days and a convoluted mass by 151 days gestation. The cords remained 0.05 to 0.06 in diameter with no lumen. Lumen formation in the rete cords was first observed at 72 days gestation at the anterior end of the rete, and gradually became complete within the testis by about 160 days.

The three regions of the epididymis were established by 88 days gestation. The caput epididymis consisted of nine to eleven

mesonephric tubules and the anterior end of the mesonephric duct located on the antero-dorsal surface of the testis. The corpus epididymis consisted of the portion of the mesonephric duct attached to the dorso-lateral surface of the testis by the mesorchium. The cauda epididymis was the portion of the mesonephric duct caught in the ventral surface of the gubernaculum posterior to the testis.

The gubernaculum, present as a connective tissue ligament at 55 days, changed to a homogenous mass of collagenous connective tissue fibers by 121 days. The gubernaculum increased in length from 5.6 mm to 24 mm as the testis migrated through the abdominal cavity, then regressed as the testis descended within the recessus vaginalis, forming a fibrous connection between the testis and the wall of the tunica vaginalis by 262 days gestation. The recessus vaginalis formed a passageway into which the testis descended, and filled out the scrotum by 121 days gestation.

Testis descent was divided into two phases: (1) posterior migration within the abdominal cavity, and (2) ventral descent within the recessus vaginalis. The testis was ventral to the anterior half of the metanephros at 55 days gestation, and migrated posteriorly to the internal inguinal ring by 101 days gestation. The testis was suspended within the abdominal cavity by the mesorchium and did not migrate retroperitoneally. Disproportionate increases in length between the gubernaculum and the recessus vaginalis were probably the factors in this process. The gubernaculum was attached firmly to the wall of the

processus vaginalis and as the processus expanded tension resulted on the gubernaculum drawing the testis towards and into the recessus vaginalis.

The testis passed through the inguinal ring into the recessus vaginalis by 106 days and by 151 days had settled into the scrotum. Five main factors appeared to be involved in the passage through the inguinal ring and in further descent;

(1) intra-abdominal pressure coupled with (2) increased length of the recessus vaginalis while (3) the gubernaculum is shortened and (4) pressure from the aponeurosis of the external oblique muscle and the developing abdominal tunic and (5) increase in size and weight of the testis itself.

The processus vaginalis could be referred to as the tunica vaginalis after the descent of the testis into the scrotum. There can be no rational subdivision of this tunica into tunic vaginalis propria and communis since the testis was encapsulated by the original tunica albuginea which was covered by a coelomic epithelium, originally the germinal epithelium.